Productivity is a poor predictor of plant species richness

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Abstract: For more than 30 years, the relationship between net primary productivity and species richness has generated intense debate in ecology about the processes regulating local diversity. The original view, which is still widely accepted, holds that the relationship is hump-shaped, with richness first rising and then declining with increasing productivity. Although recent meta-analyses questioned the generality of hump-shaped patterns, these syntheses have been criticized for failing to account for methodological differences among studies. We addressed such concerns by conducting standardized sampling in 48 herbaceous-dominated plant communities on five continents. We found no clear relationship between productivity and fine-scale (meters−2) richness within sites, within regions, or across the globe. Ecologists should focus on fresh, mechanistic approaches to understanding the multivariate links between productivity and richness.

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Productivity is a poor predictor of plant species richness

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For over 30 years, the relationship between net primary productivity and species richness has generated intense debate in ecology about the processes regulating local diversity. The original view, still widely accepted, holds that the relationship is hump-shaped, with

richness first rising and then declining with increasing productivity. Although recent meta-analyses questioned the generality of hump-shaped patterns, these syntheses have been criticized for failing to account for methodological differences among studies. We addressed such concerns by conducting standardized sampling in 48 herbaceous-dominated plant communities on five continents. We found no clear relationship between productivity and fine-scale (m^{-2}) richness within sites, within regions, or across the globe. Ecologists should focus on novel, mechanistic approaches to understand the multivariate links between productivity and richness.

For over three decades, ecologists have debated the role of primary productivity in regulating plant species richness at fine spatial scales *(1, 2)*. Although some studies have advocated multivariate approaches *(3-5)*, much of the debate remains focused on evidence for a single, general relationship between productivity and richness. This classic productivity-richness relationship (PRR) is hump-shaped, with richness increasing at low to intermediate levels of productivity and decreasing at high productivity *(6)*. The mechanisms invoked to explain the decreasing phase of the PRR in terrestrial plant communities have attracted the greatest controversy and include disturbance *(3, 7),* competitive exclusion mediated by shifts in the identity or heterogeneity of limiting resources *(8-10)*, as well as evolutionary history and dispersal limitation *(11).*

However, the theoretical justification for a hump-shaped PRR has been challenged *(12)* and the empirical evidence is mixed. For example, recent meta-analytical syntheses concluded that evidence for a single, canonical pattern was weak *(13-15)*. A large percentage of studies exhibited negative, U-shaped or nonsignificant PRR's in addition to unimodal and positive linear patterns, and the frequency of these various patterns depended on taxon and

spatial scale. Subsequent critiques of the meta-analyses argued that the apparent lack of generality in PRR's might simply reflect methodological inconsistencies among the field studies *(16, 17)*. First, PRR studies vary widely in their choice of both the grain (the area of the sampling unit) and extent (the area over which sampling units are spread) *(15, 18)*. Because of the strong effects of area and heterogeneity on richness, such differences in scale confound cross-study comparisons *(19)*. Second, many of the studies included in PRR meta-analyses did not measure primary production directly, but used weakly related surrogates such as latitude, temperature, or altitude *(14)*.

We assessed the generality of the PRR and addressed previous methodological inconsistencies by conducting standardized, observational sampling in 48 herbaceous-dominated plant communities on five continents *(20)* (Fig. 1, Supplementary Table S1). We sampled plant species richness in standard 1-m^2 quadrats located in blocks of 10 plots, holding grain constant and minimizing differences in extent across sites. In addition, we used the same protocol at all sites for estimating aboveground net primary production (ANPP) as peak growing season live biomass, an effective measure of ANPP in herbaceous vegetation *(21)*, especially when consumption by herbivores is low (Fig. S1).

Previous work indicated that the form of the PRR might vary with the spatial extent of sampling. While significant PRRs have been observed at spatial extents ranging from individual plots located within one community to means of sites spread across continents, the hump-shaped pattern has emerged most frequently in studies that cross community boundaries *(14, 22)*. PRRs described within communities may be weaker because of the potential for limited variation in productivity among sampling plots as well as measurement error on individual samples *(22)* , and because mechanisms involving variation in species pools and dispersal are

excluded. We tested for scale-dependence by characterizing the shape of the PRR at three spatial extents: (i) The within-site extent compares richness and productivity sampled in individual plots. (ii) The regional extent compares site level averages for 1-m² richness and productivity among sites occurring within a biogeographic province. (iii) The global extent compares site level averages for richness and productivity among all sites.

The 48 within-site PRR's took all possible shapes in parametric regressions of species richness on productivity (Fig. 2, Fig. S2, Table S2). The most common relationship was nonsignificant (34 sites), five sites had a positive linear pattern, five sites had a negative linear pattern, three sites were concave up (U-shape) and one site was concave down (the classical hump shape). Repeating this analysis with quasipoisson regression *(20)* gave similar results (34 nonsignificant, five positive linear, six negative linear, two concave up, and one concave down). We did not find factors that explained the variation in the shape of the within-site PRRs. For example, if unproductive sites had positive linear PRRs and highly productive sites had negative PRRs, then there should be a correlation between site level productivity and the slope of the within-site linear relationship *(18)*. We found no such pattern (r=0.07, df=46, P=0.62). Nor were sites that spanned larger ranges in productivity more likely to show significant PRR's. Specifically, the probability of finding a non-null PRR was unrelated to the range of ANPP within a site (logistic regression P=0.20).

We tested the regional relationship between site level average species richness m^{-2} and average biomass production in the three biogeographic provinces of North America in which we had more than four sites (Fig. 3). For the 11 Pacific coast sites, located west of the Cascade/Sierra mountain ranges and dominated by non-native species (along with one salt marsh), there was no significant quadratic (t=-1.0, P=0.33) or linear (t=-0.27, P=0.79) effect of

productivity on richness. Removing the highly productive salt marsh site did not change this result. Results for the seven Intermountain West sites located between the Cascade/Sierra and Rocky Mountains were similar: Neither the quadratic (t=0.52, *P*=0.63) nor linear (t=0.14, *P*=0.89) effects of productivity were significant, and removing the one site grazed by domestic livestock did not change this result. For the 13 Central Region grassland sites east of the Rockies and west of the Appalachian Mountains, we did find evidence of a hump shape, with a significant quadratic effect of productivity on richness (t=-2.35, *P*=0.041). However, when we removed five sites of anthropogenic origin (restored prairies, pastures, or old fields), the quadratic term was no longer significant (t=-0.177, *P*=0.87) while the linear term was significant (t=2.5, *P*=0.046).

At the global extent (Fig. 3), the quadratic effect of productivity on richness was significant (t=-2.39, *P*= 0.021). However, this hump-shaped model, which ignored uncertainty in estimates of site means, explained little variation in average species richness (R^2=0.11). Furthermore, the pattern was sensitive to land-use history. When we removed 9 sites of anthropogenic origin and the one salt marsh, the quadratic effect was no longer significant (t=-1.36, *P*=0.18), but a positive linear effect was significant (t=2.61, *P*=0.013).

An alternative hypothesis states that productivity sets the upper limit on richness, with stochastic forces such as disturbance causing deviations below this limit *(3, 23)*. We tested for a hump-shaped constraint on maximum richness by conducting quantile regressions on our data at within-site and global extents (we did not have sufficient data to address the regional extent). At the within-site extent, results for the 0.95 quantile regressions were similar to our standard regression analysis, with 39 nonsignificant tests, two positive linear, five negative linear, one concave up, and one concave down pattern (Figure S2). Using lower quantiles

(0.7,0.8,0.9) generated fewer significant PRRs. At the global extent (Fig. 3), the quadratic effect was not significant (t=-1.63, *P*=0.11); instead a positive linear trend emerged (t=2.19, *P*=0.034). Testing the relationship between mean productivity at a site and maximum richness observed at that site (Fig. S3) produced a similar nonsignificant quadratic effect (t=-1.50, *P*=0.14) and marginally significant linear effect (t=2.01, *P*= 0.051).

Overall, we found no consistent, general relationship between productivity and richness of herbaceous-dominated plant communities at the local, regional or global extent. Using both standard and quantile regressions, nonsignificant relationships were most common. While linear or hump-shaped patterns occurred in particular cases, no strong correlates explained these idiosyncrasies. Furthermore, consideration of land-use history and management changed the form of the regional and global scale relationships. Despite using consistent and appropriate data collection methods, our results show even less support for a general PRR than did previous synthesis efforts based on meta-analysis *(13-15)*, indicating that inadequate or non-comparable data are not the explanation for the lack of a general PRR.

If theory provided a strong prediction for the form of the PRR, then deviations from the expected pattern would be informative. However, ecologists have proposed many competing models that predict every form of the PRR *(12)*. Furthermore, recent work has emphasized that productivity does not have a direct, mechanistic effect on fine-scale species richness, but rather a complex set of interactions links the two variables *(5, 24)*. For example, productivity and richness each respond to the supply rate as well as the stoichiometry of resources *(25-27)*, with variation in these factors leading to different forms of the PRR. In addition, richness may respond more strongly to disturbance, habitat heterogeneity and biogeographic and assembly history *(3, 11, 28-30)* than to productivity. Finally, richness is not simply a function of

188 productivity, but may feedback to influence productivity *(31)*. The weak and variable PRR's we found are consistent with these hypotheses.

190 Rather than investing continued effort in attempting to identify a general PRR, ecologists should focus on more sophisticated approaches already available for investigating the 192 complex, multivariate processes that regulate both productivity and richness *(5, 25, 26)*. Coordinated, global networks represent a research approach that will be invaluable not only for 194 addressing longstanding debates about the generality of empirical patterns but also for testing the underlying mechanisms.

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Figure captions:

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Fig. 1. Locations of the 48 Nutrient Network sites that provided data for this study. Numbers
202 correspond to the Code column in Table S1. Colors and symbols represent the distinct biogeographic regions also shown in Fig. 3.

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Fig. 2. Within-site relationships between productivity, measured as peak live biomass (dry
206 weight), and species richness. The inset shows the frequencies of relationships that were nonsignificant (NS, black lines), positive or negative linear (blue lines), and concave up (+) or
208 down (-) (red curves). Statistical results and separate figures for each of the 48 sites are available in Table S2 and Figure S1, respectively. The marginal histograms show the frequency of species
210 richness and peak live biomass across all sites.

212 **Fig. 3.** The global relationship between mean productivity, measured as peak live biomass (dry weight), and mean species richness m^{-2} at each site. White dots indicate managed sites (burned
214 regularly or grazed by domestic livestock) and crosses indicate sites of anthropogenic origin (pastures, old fields and restored prairies). The solid curve shows the quadratic relationship
216 between productivity and richness with all sites included; the dotted line shows the linear relationship that remains when the anthropogenic sites are removed; the dashed line shows the
218 0.95 quantile regression with all sites included.

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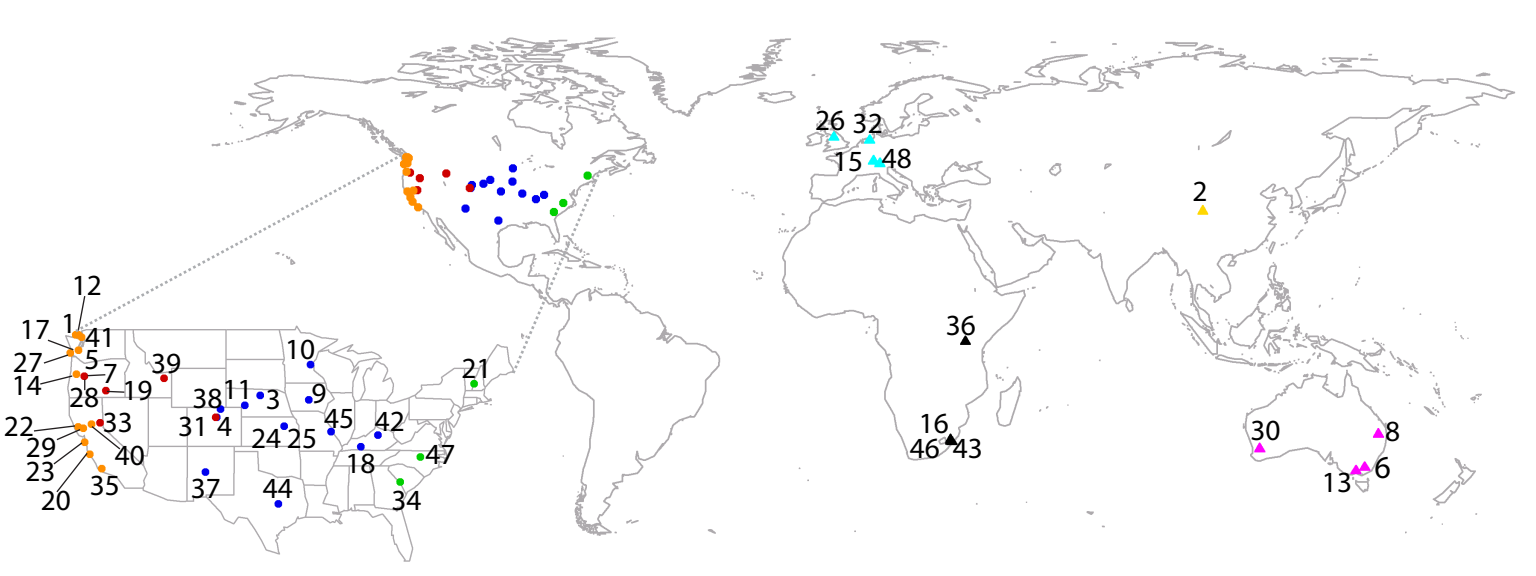
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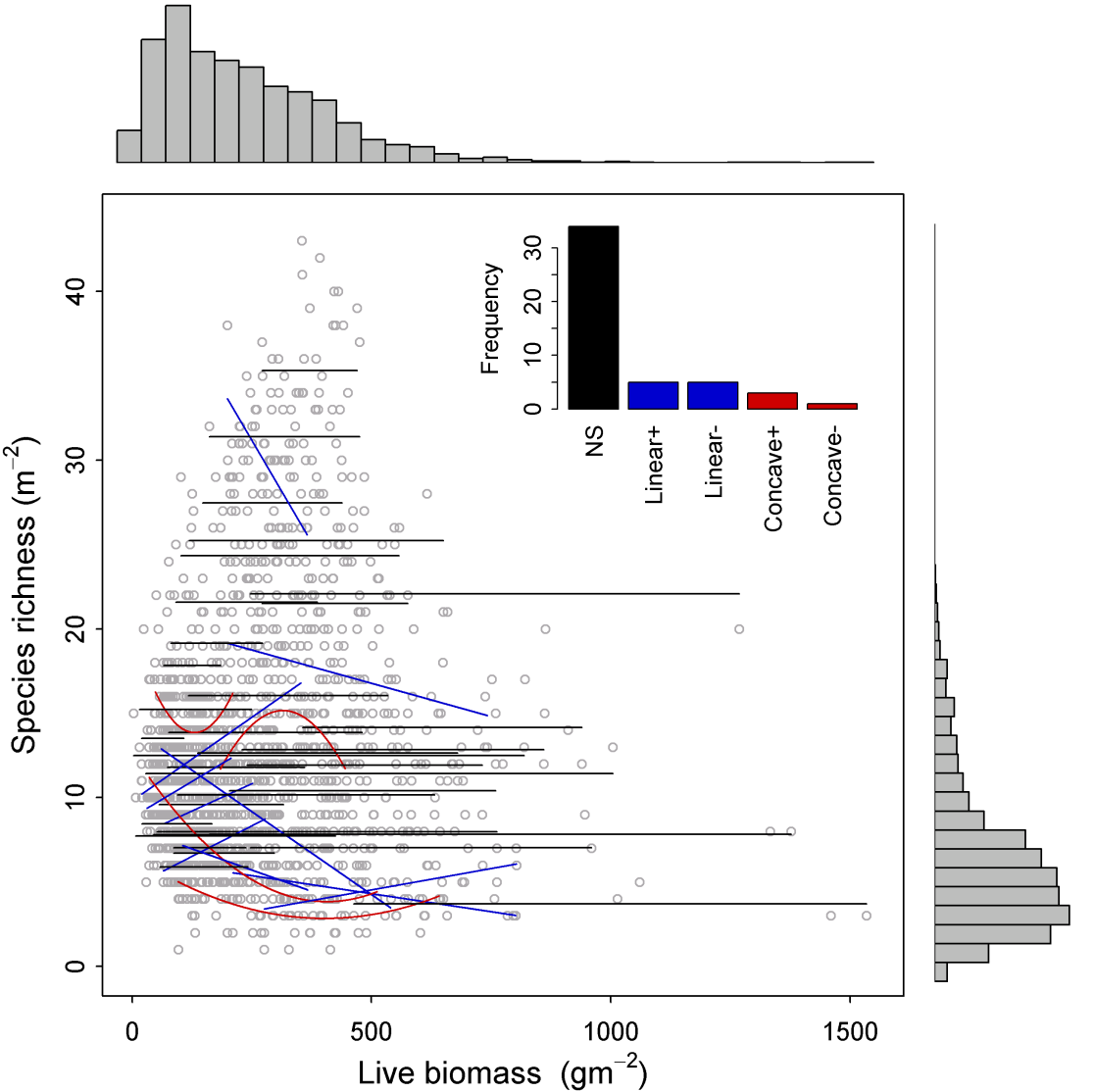
Species richness (m^{-2})
Live biomass (gm^{-2})
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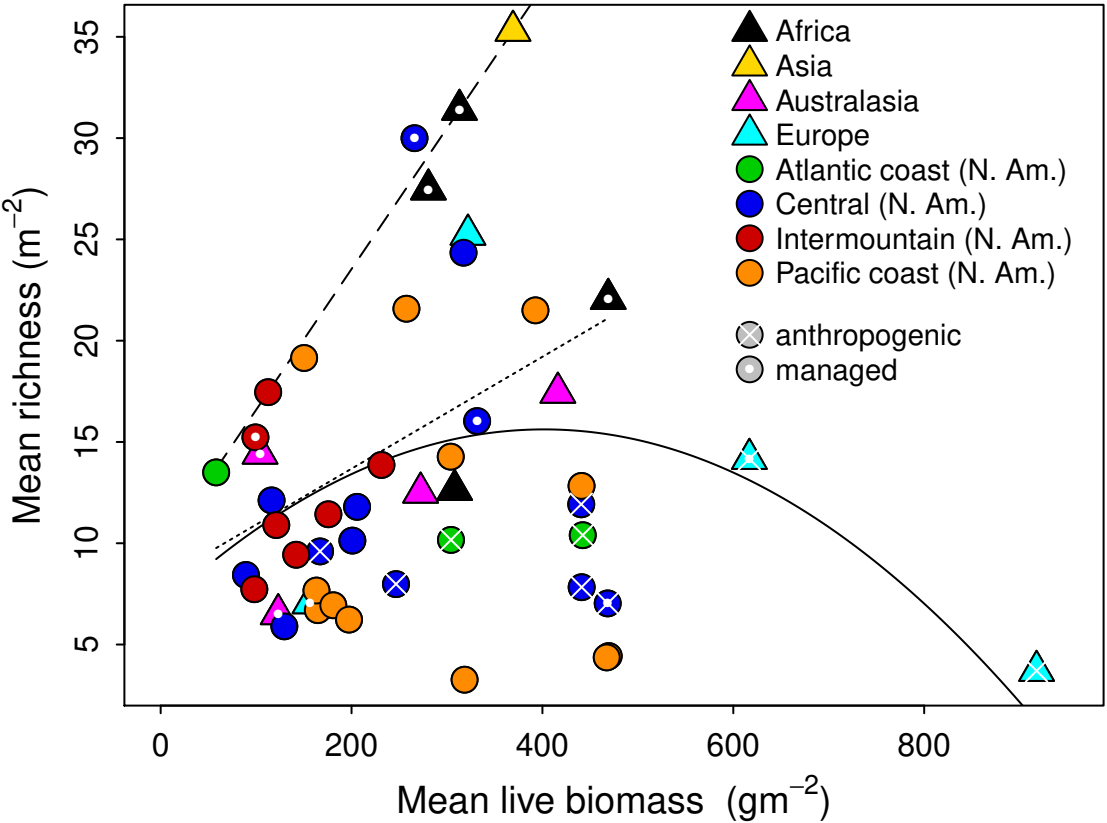
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Mean richness (m^{-2})
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200
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Supporting Online Material for

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Materials and Methods

Site selection

Each site in the Nutrient Network is dominated by low-statured, primarily herbaceous vegetation and is representative of a particular ecosystem (e.g., shortgrass steppe, tallgrass prairie, salt marsh, alpine tundra). All sites were located in a patch of relatively homogeneous vegetation large enough to accommodate the >1000 m^2 study footprint. Sites were not excluded based on natural disturbances such as fire, but such disturbances were recorded at each site. Most sites sampled vegetation in 2007, though 12 sites sampled in 2008 or 2009 (Table S1). The standard design was a completely randomized block design with three blocks and 10 plots per block at each site, though three of our sites had less than three blocks, three sites had more than three blocks and one site with 40 plots used a completely random design. Four sites are grazed by livestock and two sites were burned prior to sampling as part of the traditional site management. Each plot was 5 x 5 m separated by 1 m walkways.

Species richness

At all sites, a single 1 x 1-meter subplot within each 5 x 5-m plot was permanently marked and sampled at peak biomass. Areal cover was estimated using a modified Daubenmire method *(32)*, in which cover was recorded to the nearest 1% for each species rooted in the plot. Cover estimates also included woody overstory, litter, bare soil, and rock. Sites with strong seasonal variation in composition were sampled twice during the season to assemble a complete list of species.

Productivity

Immediately adjacent to the permanent 1 x 1-m cover plot, growing season peak standing crop was estimated destructively by clipping at ground level all aboveground biomass of individual plants rooted within two 0.1-m^2 (10 x 100 cm) strips. Biomass was sorted into current (live and recently senescent material) and previous year's growth. For shrubs and sub-shrubs, all leaves and current year's stems were collected. All biomass was dried at 60°C for 48 hrs prior to weighing to the nearest 0.01 g. We used the current year's biomass as our estimate of aboveground net primary production (ANPP) *(33,34)*. All sites used this protocol to estimate productivity, except for the Sevilleta, NM, site which relied on species-specific allometric relationships *(35)*.

In communities where herbivores consume a significant fraction of production, our method will underestimate ANPP. A correlation between the size of this underestimate and ANPP could bias the relationship between productivity and richness. We evaluated this potential bias using plot-level mammalian herbivore exclosures constructed at 29 of the 48 sites included in our analysis (exclosures were installed the year after collection of the observational data that is the main focus of this study). Exclosures used barbed wire up to 2 m high to exclude large mammals with a bottom overlay of hardware cloth folded against the ground to deter small mammals. We calculated the percentage of ANPP consumed by herbivores at the block level as

$$100 \times (B_{exclosure} - B_{herbivory}) / B_{exclosure}$$

where *Bexclosure* and *Bherbivory* are live biomass inside and outside of exclosures, respectively. We then averaged this measure of consumption across blocks within each site. We set negative values of consumption, reflecting higher average biomass outside the exclosures, equal to zero. Percent consumption was less than 20% for all but four sites (two of which had only one exclosure) and was uncorrelated with ANPP (Figure S1).

Statistical analysis

In preliminary analyses, we noticed potential outlier data points. We evaluated and removed these outliers using a two-step procedure. First, we flagged data points with values of Cook's distance (a measure of influence) greater than 1 in the within-site quadratic regressions. Second, we tested whether removal of these data points altered the hypothesis tests of the within-site regressions (as described below). We removed four data points (from four sites) that changed the outcome of a hypothesis test as follows: one concave-down pattern became positive linear, one nonsignificant became concave-down, one linear became nonsignificant, and one concave-up became nonsignificant. All of our final analyses were conducted after removal of the outliers.

To explore the relationship between productivity and species richness among plots within each site, we first fit a model in which species richness was a linear and quadratic function of live biomass. If the quadratic term was not significant at the $\alpha=0.1$ level, we dropped the quadratic term and fit a model containing only the linear term. If the linear term was not significant at $\alpha=0.1$, we classified the relationship as nonsignificant. This approach, which is consistent with previous meta-analyses *(13,14)*, emphasizes hypothesis testing of the quadratic term rather than overall model fit. Nevertheless, we found that the results were consistent with an information-theoretic approach using Akaike's Information Criteria (not shown). We chose the liberal $\alpha=0.1$ level of significance because we wanted our conclusions about the lack of a general pattern to be conservative.

Our response variable, counts of species richness, is not strictly normally-distributed (Gaussian). Therefore, we first fit Poisson regressions in a generalized-linear model framework. After finding that the data for almost all the sites were under-dispersed (deviance/df $<<1$), we then refit all the models with both Gaussian and quasipoisson approaches. These two approaches led to almost identical patterns in the frequency of nonsignificant, linear, and quadratic models. Given that the choice of error distribution did not affect our conclusions, we chose to focus on the results from the Gaussian models, consistent with previous work on PRR's *(14)*, but we do describe the quasipoisson results in the main text.

To describe the regional and global scale across-site relationships between productivity and species richness, we regressed the mean number of species m^{-2} on the mean biomass production m^{-2} at each site. We then repeated the hypothesis tests of the quadratic and linear terms as in the within-site analysis described above. We repeated these regressions for subsets of sites with different management histories. We did not conduct additional Poisson regressions for these site-averaged data because they met the assumptions of normality better than the individual plot data.

We performed quantile regressions to test for relationships between maximum richness and productivity at the within-site and global scales. We used the rq() function

of the quantreg package in R v.2.10.0. Although we only report results for the 0.95 quantile, we also tested the 0.7, 0.8 and 0.9 quantiles. We performed hypothesis tests using the bootstrap option with 10000 replications.

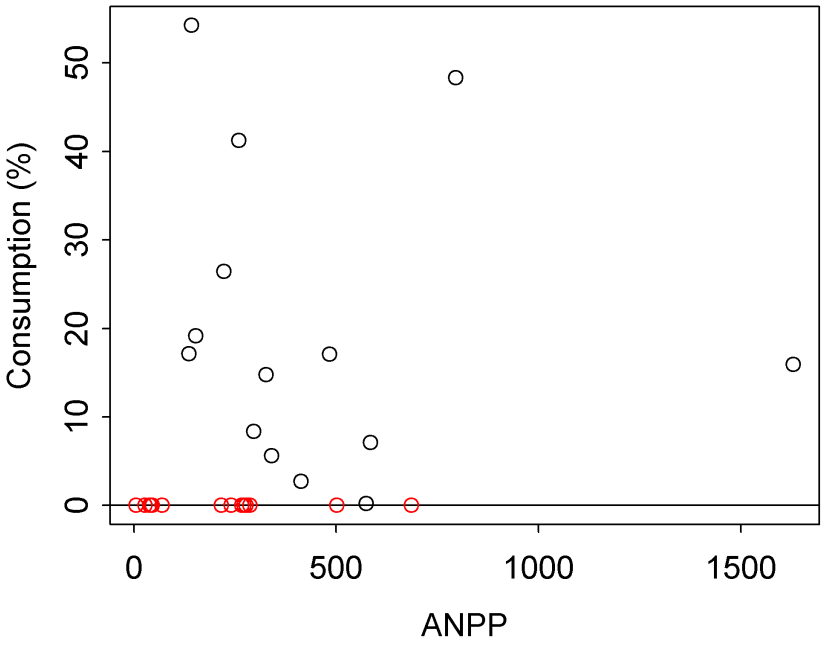

Fig. S1.

No correlation between consumption and aboveground net primary production (ANPP) estimated in exclosures at 29 sites. Consumption (%) is estimated as 100*(biomass in exclosures – biomass in open plots)/(biomass in exclosures). The red symbols indicate sites where consumption was negative (higher biomass outside the exclosures than inside); we set these values to zero.

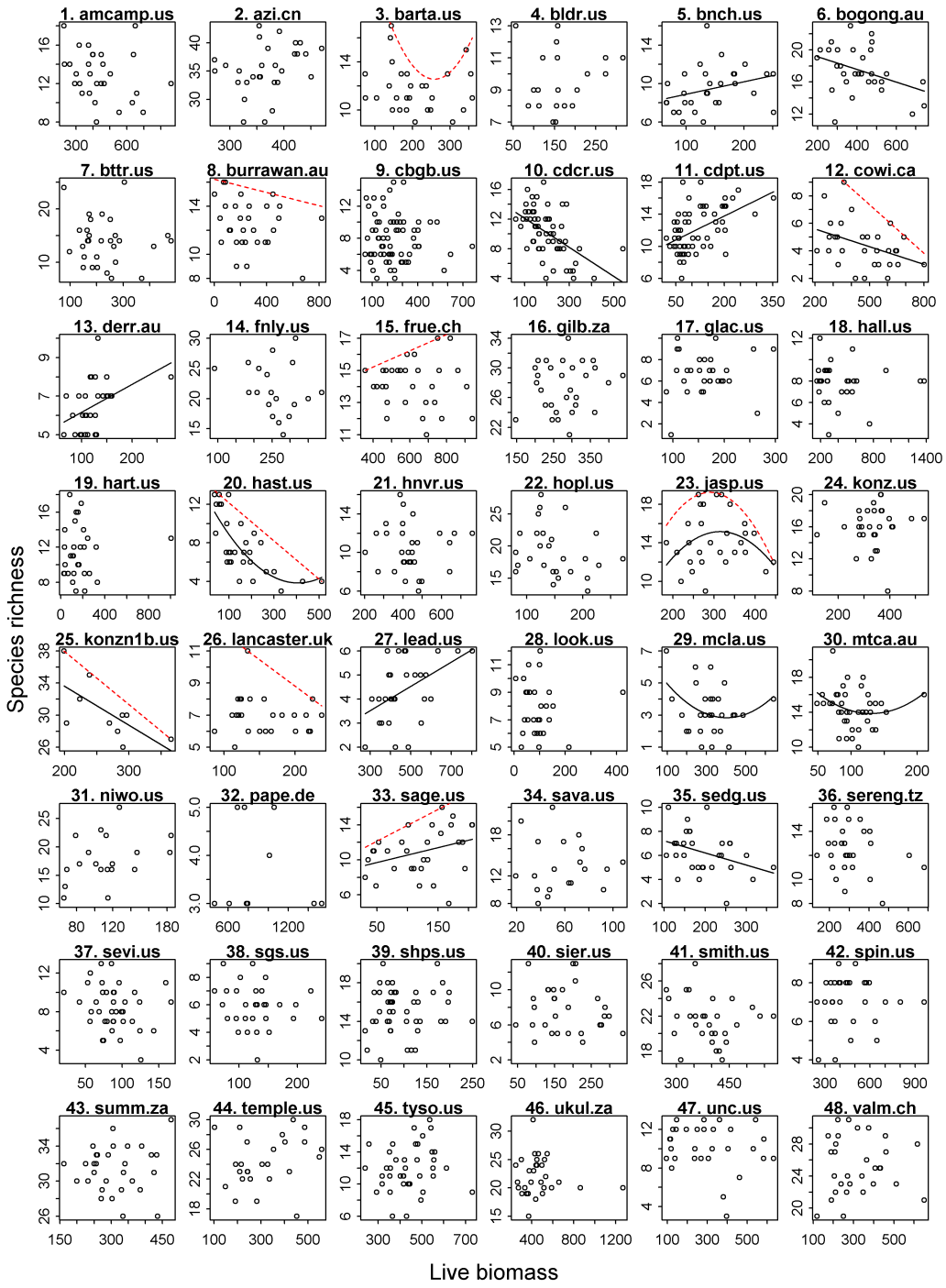

Fig. S2

Within-site productivity-species richness relationships. Regression lines (black) are shown only for models with significant (P<0.1) linear or quadratic terms. Dashed red lines show quadratic regressions (0.95 quantile) with significant (P<0.1) linear or quadratic terms. Titles refer to the Code column in Table S1.

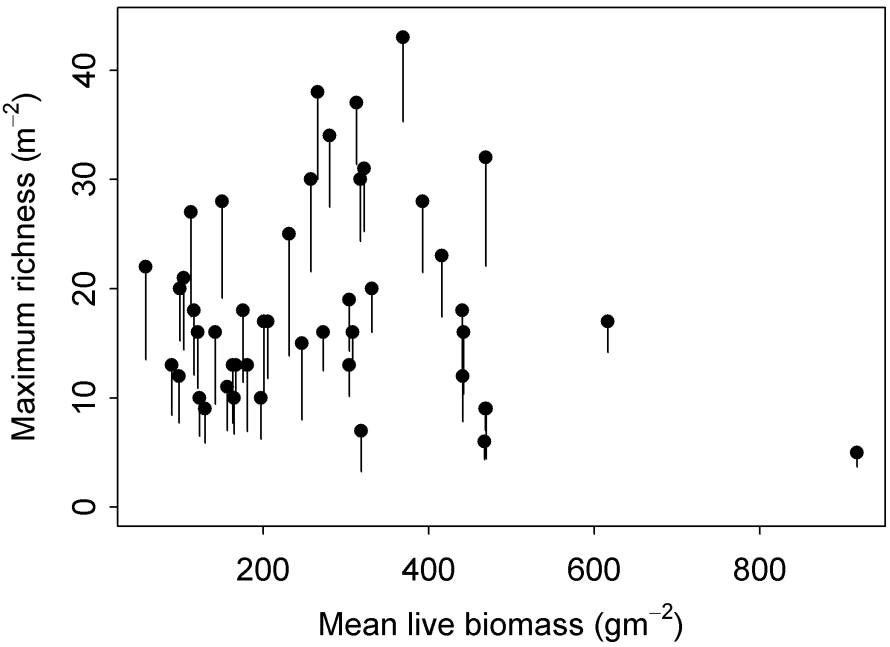

Fig. S3

The relationship between mean productivity and maximum richness (filled circles) at each site. Vertical lines indicate the difference between mean and maximum richness at each site.

Table S1
Additional information on the 48 study sites.

Site	Code	Year	Habitat	Nation	Lat.[1]	Lon.[2]	m.a.s.l.[3]	PPT[4]	Winter low[5]	Summer high[6]
amcamp.us	1	2007	MESIC GRASSLAND	USA	48.47	-123.01	41	672	2.0	21.5
azi.cn	2	2007	ALPINE GRASSLAND	China	33.58	101.53	3500	620	-13.0	32.0
barta.us	3	2007	MIXEDGRASS PRAIRIE	USA	42.24	-99.65	767	568	-13.1	29.9
bldr.us	4	2008	SHORTGRASS PRAIRIE	USA	39.97	-105.23	1633	482	-6.0	29.5
bnch.us	5	2007	MONTANE MEADOW	USA	44.28	-121.97	1500	2160	-1.3	30.2
bogong.au	6	2006	ALPINE GRASSLAND	Australia	-36.87	147.25	1760	1217	-3	17.4
bttr.us	7	2007	MONTANE MEADOW	USA	44.28	-121.96	1500	2160	-1.3	30.2
burrawan.au	8	2008	SEMIARID GRASSLAND	Australia	-27.73	151.14	425	600	4.7	33.5
cbgb.us	9	2009	TALLGRASS PRAIRIE	USA	41.79	-93.43	275	891	-11.8	30.4
cdcr.us	10	2007	TALLGRASS PRAIRIE	USA	45.40	-93.20	270	800	-16.8	26.9
cdpt.us	11	2007	SHORTGRASS PRAIRIE	USA	41.20	-101.63	965	470	-9.4	32.1
cowi.ca	12	2007	SAVANNA	Canada	48.46	-123.38	50	1039	-1.1	23.3
derr.au	13	2007	SEMIARID GRASSLAND	Australia	-37.81	144.79	38	544	4.9	25.6
fnly.us	14	2007	MESIC GRASSLAND	USA	44.41	-123.28	68	1200	0.9	27.3
frue.sw	15	2008	PASTURE	Switzerland	47.37	8.55	995	1102	-8.6	26.9
gilb.za	16	2009	MESIC GRASSLAND	South Africa	-29.28	30.29	1748	867	3.0	28.0
glac.us	17	2007	MESIC GRASSLAND	USA	46.87	-123.03	33	1300	0.6	25.3
hall.us	18	2007	TALLGRASS PRAIRIE	USA	36.96	-86.73	194	1282	-4.1	31.6
hart.us	19	2007	SHRUB STEPPE	USA	42.72	-119.50	1508	305	-5.7	30.0
hast.us	20	2007	ANNUAL GRASSLAND	USA	36.20	-121.55	750	550	6.3	20.1
hnvr.us	21	2007	OLD FIELD	USA	43.42	-72.14	271	919	-13.5	27.4
hopl.us	22	2007	ANNUAL GRASSLAND	USA	39.01	-123.06	416.67	940	2.8	32.6

Site	Code	Year	Habitat	Nation	Lat.[1]	Lon.[2]	m.a.s.l.[3]	PPT[4]	Winter low[5]	Summer high[6]
jasp.us	23	2007	ANNUAL GRASSLAND	USA	37.41	-122.24	120	655	2.4	31.2
konz.us	24	2008	TALLGRASS PRAIRIE	USA	39.08	-96.58	440	835	-9.0	33.0
konzn1b.us	25	2007	TALLGRASS PRAIRIE	USA	39.08	-96.58	NA	835	-9.0	33.0
lancaster.uk	26	2008	PASTURE	UK	53.9	-2.62	180	1222	-2.6	25.0
lead.us	27	2007	SALT MARSH	USA	46.61	-124.05	2	2044	2.3	18.7
look.us	28	2007	MONTANE MEADOW	USA	44.21	-122.13	1500	2314	-1.3	30.2
mcla.us	29	2007	ANNUAL GRASSLAND	USA	38.86	-122.41	550	650	-0.1	32.4
mtca.au	30	2008	SAVANNA	Australia	-31.78	117.61	285	352	1.0	40.0
niwo.us	31	2007	ALPINE GRASSLAND	USA	39.99	-105.38	3050	930	-16.4	16.3
pape.de	32	2007	OLD FIELD	Germany	53.09	7.47	0.5	770	0.6	22.3
sage.us	33	2007	MONTANE MEADOW	USA	39.43	-120.24	1920	850	-9.8	26.2
sava.us	34	2007	SAVANNA	USA	33.34	-81.65	71	1000	0.8	34.3
sedg.us	35	2007	ANNUAL GRASSLAND	USA	34.70	-120.02	550	380	4.2	32.9
sereng.tz	36	2008	SAVANNA	Tanzania	-2.25	34.51	1536	789	13.1	29.3
sevi.us	37	2007	DESERT GRASSLAND	USA	34.36	-106.69	1600	250	-8.1	33.3
sgs.us	38	2007	GRASSLAND	USA	40.82	-104.77	1650	299	-10.6	31.4
shps.us	39	2007	SHRUB STEPPE	USA	44.00	-112.00	910	325	-12.0	29.5
sier.us	40	2007	ANNUAL GRASSLAND	USA	39.24	-121.28	333	711	3.2	35.7
smith.us	41	2007	MESIC GRASSLAND	USA	48.21	-122.62	62	550	1.3	21.7
spin.us	42	2007	PASTURE	USA	38.14	-84.50	271	1166	-4.4	29.9
summ.za	43	2009	MESIC GRASSLAND	South Africa	-29.81	30.72	679	809	9.1	27.1
temple.us	44	2007	TALLGRASS PRAIRIE	USA	31.10	-97.34	194	870	8.0	40.0
tyso.us	45	2007	OLD FIELD	USA	38.52	-90.56	169	1090	-7.6	31.3

Site	Code	Year	Habitat	Nation	Lat.[1]	Lon.[2]	m.a.s.l.[3]	PPT[4]	Winter low[5]	Summer high[6]
ukul.za	46	2009	MESIC GRASSLAND	South Africa	-29.67	30.40	842.5	838	8.8	26.4
unc.us	47	2007	OLD FIELD	USA	35.91	-79.06	141	1210	-2.6	31.7
valm.sw	48	2008	ALPINE GRASSLAND	Switzerland	46.63	10.37	2320	950	-15.7	17.0

[1]Latitude

[2]Longitude

[3]meters above sea level

[4]mean annual precipitation (mm)

[5]Mean minimum temperature in January (northern hemisphere) or July (southern hemisphere)

[6]Mean maximum temperature in July (northern hemisphere) or January (southern hemisphere)

Table S2.
Statistical results for quadratic regressions at the within-site level.

Site	Mean live biomass	Mean species richness	Linear term			Quadratic term		
			coefficient	t	*P*	coefficient	t	*P*
amcamp.us	441	12.8	-0.0041	-1.34	0.191	0.00002	0.96	0.345
azi.cn	369	35.3	0.0249	1.64	0.112	0.00028	1.12	0.274
barta.us	206	11.8	-0.0034	-0.74	0.466	0.00005	0.98	0.333
bldr.us	167	9.6	0.0028	0.44	0.667	0.00013	1.59	0.131
bnch.us	142	9.4	0.0129	1.72	0.096	-0.00019	-1.49	0.148
bogong.au	416	17.4	-0.0079	-2.20	0.036	-0.00002	-1.04	0.307
bttr.us	231	13.9	-0.0051	-0.61	0.547	0.00007	1.06	0.299
burrawan.au	272	12.5	-0.0025	-1.27	0.213	0.00001	0.86	0.399
cbgb.us	247	8.0	-0.0017	-0.65	0.518	0.00000	-0.33	0.740
cdcr.us	201	10.1	-0.0196	-4.82	0.000	0.00004	1.36	0.179
cdpt.us	116	12.1	0.0198	4.39	0.000	-0.00002	-0.43	0.668
cowi.ca	469	4.4	-0.0043	-2.28	0.031	0.00000	0.33	0.741
derr.au	123	6.5	0.0145	2.59	0.015	-0.00006	-0.89	0.381
fnly.us	258	21.6	-0.0135	-0.88	0.390	0.00011	0.70	0.491
frue.ch	617	14.2	-0.0007	-0.40	0.693	0.00000	-0.24	0.811
gilb.za	281	27.5	0.0068	0.73	0.469	0.00001	0.10	0.924
glac.us	165	6.7	0.0039	0.53	0.602	-0.00001	-0.11	0.910
hall.us	441	7.8	-0.0003	-0.30	0.766	0.00000	0.87	0.393
hart.us	176	11.4	0.0011	0.34	0.736	0.00000	0.33	0.745
hast.us	163	7.7	-0.0177	-4.75	0.000	0.00005	2.31	0.029
hnvr.us	442	10.4	-0.0007	-0.17	0.863	0.00002	0.82	0.417
hopl.us	150	19.1	-0.0197	-1.27	0.216	-0.00007	-0.26	0.796
jasp.us	304	14.3	0.0001	0.01	0.994	-0.00020	-1.89	0.070
konz.us	332	16.0	0.0005	0.08	0.937	0.00002	0.53	0.603
konzn1b.us	266	30.4	-0.0484	-2.54	0.034	0.00021	0.63	0.551
lancaster.uk	156	7.0	-0.0040	-0.73	0.474	-0.00008	-0.54	0.596
lead.us	467	4.4	0.0051	2.86	0.008	0.00000	-0.37	0.714
look.us	98	7.7	-0.0005	-0.09	0.925	0.00004	1.15	0.259
mcla.us	318	3.3	-0.0026	-1.04	0.308	0.00002	1.79	0.084
mtca.au	104	14.4	-0.0089	-0.78	0.441	0.00036	1.74	0.090
niwo.us	113	17.8	0.0441	1.64	0.120	-0.00043	-0.64	0.531
pape.de	918	3.7	-0.0003	-0.36	0.729	0.00000	-1.70	0.133
sage.us	121	10.9	0.0169	1.90	0.068	0.00011	0.59	0.558

Site	Mean live biomass	Mean species richness	Linear term			Quadratic term		
			coefficient	T	*P*	coefficient	T	*P*
sava.us	58	13.5	-0.0029	-0.08	0.938	-0.00003	-0.02	0.982
sedg.us	197	6.2	-0.0101	-2.06	0.049	0.00002	0.26	0.800
sereng.tz	308	12.6	-0.0048	-1.54	0.135	0.00000	-0.05	0.960
sevi.us	89	8.4	-0.0153	-1.25	0.220	0.00031	1.17	0.249
sgs.us	130	5.9	-0.0057	-0.84	0.407	0.00011	0.96	0.347
shps.us	99	15.2	0.0051	0.83	0.411	-0.00003	-0.31	0.759
sier.us	181	7.8	-0.0050	-0.76	0.454	-0.00011	-1.26	0.219
smith.us	393	21.5	-0.0066	-1.01	0.319	0.00011	1.66	0.109
spin.us	468	7.0	0.0004	0.24	0.811	-0.00001	-0.96	0.345
summ.za	313	31.4	0.0024	0.37	0.711	0.00008	1.02	0.318
temple.us	317	24.3	0.0059	1.11	0.276	0.00004	0.93	0.364
tyso.us	441	11.9	0.0040	0.90	0.371	-0.00002	-0.62	0.542
ukul.za	469	22.1	-0.0014	-0.44	0.663	-0.00001	-0.86	0.399
unc.us	304	10.2	-0.0024	-0.87	0.392	0.00001	0.28	0.779
valm.ch	322	25.2	0.0010	0.20	0.845	-0.00004	-1.14	0.265